SMALL FOSSIL VERTEBRATES FROM VICTORIA CAVE, NARACOORTE, SOUTH AUSTRALIA

II. PERAMELIDAE, THYLACINIDAE AND DASYURIDAE (MARSUPIALIA)

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Summary

Abundant fossil remains of marsupials and rodents have been found in Victoria Cave, near Naracoorte, South Australia. The presence of certain large, extinct herbivores in the assemblage suggests that the deposit may be of Pleistocene age. This paper describes remains of *Isoodon obesulus* (Shaw, 1797), *Perameles gunnii* Gray, 1838 and *P. bougainville* Quoy & Gaimard, 1824 (Peramelidae); *Thylacinus cynocephalus* (Harris, 1808) (Thylacinidae); *Dasyurus maculatus* (Kerr, 1792), *D. viverrinus* (Shaw, 1800), *Antechinus flavipes* (Waterhouse, 1838), *A. swainsonii* (Waterhouse, 1840), *A. stuartii* Macleay, 1841, *Sminthopsis murina* (Waterhouse, 1838) and *S. crassicaudata* (Gould, 1844) (Dasyuridae). Extensions of the previously known ranges of *P. bougainville* and *A. stuartii* are noted. The larger species are represented mainly by juveniles and it is suggested that the small mammal remains were accumulated by owls.

Introduction

Victoria Cave, in Tertiary limestone near Naracoorte (lat. 37°0′S, long. 149°48′E) has been open to tourists for many years. In 1969, the Cave Exploration Group of South Australia (CEGSA) discovered further extensive ramifications of the cave and, in one chamber, a silt deposit containing abundant skeletal remains of large animals. Many of these were later identified as remains of extinct marsupial herbivores (sthenurines and diprotodontids) and of the marsupial lion, *Thylacoleo* sp. (Wells, pers. comm.). The sthenurines and diprotodontids are believed to have become extinct at the end of the Pleistocene (Tedford 1967), and the deposit in Victoria Cave is therefore probably of Pleistocene age.

Bone chips occur in cores taken as deep as 2.5 m but the maximum depth of excavation at present is 80 cm.

The potoroines (Macropodidae), petaurids and burramyids have been described previously (Smith 1971); the present paper describes the peramelids, a thylacinid and the dasyurids.

Methods

The methods of sieving the bony remains from the silt, and their subsequent cleaning and preservation have been described (Smith 1971). Measurements of teeth have been made in the way described in that paper, with the exception that, in the peramelids only, the maximum anteroposterior lengths of mandibular molar teeth were measured on the lingual side. (The slope of the anterior cingulum from lingual side to buccal side hindered accurate measuring on the buccal side.) Additional mandible measurements were taken as follows:

Length of ascending ramus: Distance between anterior and posterior borders of the ascending ramus, from the midpoint of the posterior border and perpendicular to the ramus midline.

Breadth at $M_{\frac{1}{2}}$: Thickness of mandible below $M_{\frac{1}{2}}$.

Height at $M_{\frac{1}{2}}$: Distance from alveolar margin at middle of $M_{\frac{1}{2}}$ to inferior border of mandible, and perpendicular to the inferior border.

The taxonomy used is that of Ride (1970) unless stated otherwise.

Family PERAMELIDAE

Isoodon obesulus (Shaw, 1797)

The following features were used to distinguish fragmentary remains of *Isoodon* from *Perameles*.

(i) The hypocone of each maxillary molar (except $M^{\frac{1}{2}}$) is well developed in *Isoodon* so that in horizontal section these teeth appear as rounded

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blocks. In *Perameles* the hypocones are much smaller and $M^1_?$, $M^2_?$, and $M^3_?$ appear as truncated triangles, tapering lingually. The molar alveoli reflect the shape of the teeth, the lingual root relative to the buccal length of the tooth being much longer in *Isoodon* than in *Perameles*.

(ii) In the mandible of *Isoodon*, the anterior edge of the ascending ramus makes an obtuse angle with the horizontal ramus, whereas in *Perameles* the horizontal and ascending portions of the ramus join in a continuous smooth curve (Merrilees 1965) (Figs. 1, 2, 3).

(iii) In *Isoodon* the lingual extremity of the anterior cingulum is almost as high as the apex of the paraconid of M_2, M_3, and M_4, whereas in *Perameles* the greatest height of the anterior cingulum is much less than that of the paraconid.

Isoodon was not abundant in the deposit and adults and juveniles were about equally represented (Table 1).

Modern specimens of *I. obesulus* in the South Australian Museum vary greatly in size, and wide variations occur even in adult specimens of the same sex and locality. The length of $M^1_?$–$^3_?$ varied from 9.2 to 11.4 mm (mean 10.19, s.d. 0.72) in eight South Australian mainland specimens and the length of M^1_4–$_4$ from 12.7 to 15.8 mm (mean 14.49, s.d. 1.08). Victoria Cave specimens are smaller than modern mainland specimens (Table 2) and are almost as small as the insular subspecies, *I. o. nauticus* where, in nine specimens, the length of $M^1_?$–$^3_?$ ranged from 8.4 to 9.5 mm (mean 8.68, s.d. 0.35) and the length of M^1_4–$_4$ from 11.8 to 12.5 mm (mean 12.20, s.d. 0.28). The teeth of Victoria Cave *Isoodon* are morphologically similar to those of modern *I. obesulus*.

Wakefield (1966b and *in* Mulvaney et al. 1964) referred to a distinct, small form of *I. obesulus* from Mildura and from the Fromm's Landing archaeological excavation on the River Murray, but he gave no measurements of this form, nor of the "much larger form abundant in S. Victoria". Pleistocene specimens of *I. obesulus* from Mammoth Cave, Western Aus-

TABLE 1

Mandibular and maxillary fragments of peramelid species found in the Victoria Cave, Naracoorte. Many isolated teeth were collected but have not been included in the table.

Species	Maxillae				Mandibles				Minimum no. of individuals
	Adult		Juvenile*		Adult		Juvenile*		
	Right	Left	Right	Left	Right	Left	Right	Left	
Isoodon obesulus	4	4	—	—	8	10	7	4	17
Perameles gunnii	9	7	1	—	16	23	54	46	77
P. bougainville	11	7	5	8	30	38	32	27	70
Not determinable	2	2	3	3	5	6	9	5	15

* A specimen was considered to be juvenile if P4 and/or M4 were not fully erupted.

TABLE 2

Some dimensions of mandibles and teeth of Isoodon obesulus *from Victoria Cave.*

Dimension	Number of Specimens	Range (mm)	Mean (mm)	Standard error	Coefficient of variation
Length of ascending ramus	7	6.3—7.3	6.79	0.146	5.7
Breadth at M_2	6	2.4—2.8	2.58	0.075	7.1
Height at M_2	6	3.6—4.5	4.10	0.152	9.1
$M^1_?$–$^3_?$ length	3	9.0—9.2	9.10	0.057	1.1
P^4 length	5	2.3—2.6	2.44	0.060	5.5
P^4 breadth	5	1.2—1.5	1.38	0.049	7.9
M^1_4–$_4$ length	6	11.7—12.8	12.27	0.158	3.2

tralia, are similar in size to modern specimens from the same area (Merrilees 1965).

I. obesulus still occurs in the Naracoorte district.

Genus PERAMELES

Perameles was represented by many toothless mandibles and a few tooth-bearing maxillae and mandibles. Adult mandibles, in which P_4^4 and M_4^4 were erupted, could clearly be separated on size into two species, distinguished by depth and thickness of the mandible, length of ascending ramus, and length of teeth (compare Figs 2 and 3; and Tables 4 and 5). Juvenile mandibles of the two species overlapped in size but could be separated by the length, and especially by the width, of their molar alveoli. Maxillae, both adult and juvenile, were identified by the size of the molar alveoli.

Perameles gunnii Gray, 1838

Live specimens of the two large long-nosed bandicoots, *P. gunnii* and *P. nasuta* Geoffroy, 1804, appear quite dissimilar, the rump of *gunnii* being barred and that of *nasuta* being uniformly coloured (Ride 1970). However the skulls of the two species are similar in morphology, size and proportions. I_3^3 provides the main difference, I_3^3 of *gunnii* being double rooted, antero-posteriorly long and bucco-lingually compressed, whereas I_3^3 of *nasuta* is single rooted and caniniform (Freedman 1967). This diagnostic feature could not be used on Victoria Cave material as no premaxillae were preserved. Additional differences are that the mandible is more slender in *P. gunnii*, M_3^3 is shorter buccally and M_4^4 is shorter antero-posteriorly (Table 3). The figures given in Table 3 do not confirm Tate's (1948) statement that P_3^3 is much broader in *P. gunnii*.

Remains of the large *Perameles* from Victoria Cave conform in size with modern *P. gunnii* (Table 4) and no morphological differences were detected between fossil and modern specimens. Remains of juvenile *P. gunnii* were relatively abundant, but few adult specimens were found (Table 1).

P. gunnii is not included in a list of the modern native mammals of South Australia (Aitken 1970) although three specimens of *P. gunnii* in the South Australian Museum are registered as from South Australia (M1607 from Mt. Gambier, M1613 from "South Australia" and M3956 from the Rocks, Kougal, south-east of South Australia). All were collected between 1891 and 1893. The present range of *P. gunnii* is southern Victoria and Tasmania (Ride 1970).

Remains of *P. gunnii* were found in an aboriginal midden at Mt. Burr, South Australia (Finlayson 1966, unpublished[1]) and in a late Recent deposit in the Bat Cave at Naracoorte (Tidemann 1967).

TABLE 3

Some dimensions of mandibles and teeth in which Perameles nasuta *differs from* P. gunnii. *These figures were calculated from data given in Tables 2, 3A and 3B of Freedman & Joffe 1967a and Tables 1, 2A and 2B of Freedman & Joffe 1967b.*

Dimension examined	*Perameles nasuta*			*Perameles gunnii*		
	N	Mean (mm)	95% confidence limits of mean	N	Mean (mm)	95% confidence limits of mean
Length of ascending ramus	69	8.79	8.52—9.06	40	6.34	6.23—6.46
Breadth at M_2^2	71	3.54	3.43—3.65	41	2.82	2.76—2.90
Height at M_2^2	71	6.70	6.49—6.91	41	5.88	5.70—6.06
P_3^3 length	65	3.75	3.65—3.84	40	3.34	3.26—3.43
P_3^3 width	81	2.10	2.06—2.15	40	2.13	2.09—2.17
M^4 width	81	2.71	2.66—2.75	42	2.75	2.68—2.82
M_3^3 Buccal length	81	3.63	3.56—3.70	43	3.09	3.03—3.15
M_3^3 Lingual length	82	1.53	1.50—1.56	43	1.44	1.40—1.48
M_4^4 Anterior width	91	2.37	2.34—2.39	46	2.16	2.13—2.18
M_4^4 Posterior width	86	1.60	1.58—1.63	46	1.51	1.48—1.55
M_4^4 length	85	4.64	4.58—4.70	45	4.01	3.96—4.06

[1]Finlayson, H. H. *in* Campbell, T. D., Edwards, R. & Hossfeld, P. S. (1966).—Archaeological excavations in the Southeast of South Australia. 24 pp. Transcript, Australian Institute of Aboriginal Studies Library, Canberra.

Perameles bougainville Quoy & Gaimard, 1824

The small bandicoots from eastern, central and Western Australia have been described as several different species, but Tate (1948) suggested that *P. bougainville, fasciata, notina* and *eremiana* might be local races of a single widespread species. Generally this has been accepted (e.g. Wakefield 1966a) although Ride (1970) retained *eremiana* as a distinct species. Mean measurements of skulls and teeth are mostly larger in the south central population, *notina*, than in the western population, *bougainville* (sens. strict.), but few of the differences are significant (Freedman & Joffe 1967b).

Remains of the small species of *Perameles* from Victoria Cave are similar in size and morphology to modern specimens of *P. bougainville* in the South Australian Museum and to specimens from the Fromm's Landing archaeological excavation (Table 5).

TABLE 4

Comparisons of some dimensions of teeth and mandibles of Perameles gunnii *from Victoria Cave, with those of a modern sample from Tasmania. C.V. — Coefficient of variation.*

Dimension	Modern *P. gunnii* from Tasmania					*P. gunnii* from Victoria Cave				
	n	Range (mm)	Mean	Standard error	C.V.	n	Range (mm)	Mean	Standard error	C.V.
M⅓ width	10	3.6—4.1	3.91	.057	4.6	3	3.6—3.7	3.63	.033	1.6
M⅓ buccal length	10	2.8—3.2	3.03	.032	3.3	3	2.9—3.0	2.97	.033	1.9
M⅓ lingual length	10	1.3—1.6	1.47	.037	7.9	3	1.0—1.3	1.20	.100	14.4
M⅓–⅜ alveolar length	10	11.4—12.4	11.86	.105	2.8	4	11.4—12.4	11.80	.245	4.2
Length of ascending ramus	10	6.1—7.4	6.70	.127	6.0	10	5.2—6.2	5.75	.100	5.5
Breadth at M½	10	2.6—3.2	2.99	.060	6.4	9	2.3—2.8	2.54	.055	6.6
Height at M½	10	5.8—7.6	6.66	.153	7.3	8	4.5—6.4	5.57	.190	9.7
M¼ alveolar length	10	3.6—4.1	3.90	.056	4.5	9	3.4—4.0	3.73	.078	7.0
M⅓–¼ alveolar length	10	14.6—16.6	15.57	.172	3.5	5	15.0—15.5	15.18	.086	1.3

TABLE 5

Comparisons of some dimensions of teeth and mandibles of Perameles bougainville *from Victoria Cave with those from Fromm's Landing (specimens collected in levels 0-9).*

Dimension	*P. bougainville* from Fromm's Landing					*P. bougainville* from Victoria Cave				
	n	Range (mm)	Mean	Standard error	C.V.	n	Range (mm)	Mean	Standard error	C.V.
M⅓–⅜ length	—	—	—	—	—	4	9.1—10.4	9.60	.334	7.0
Length of ascending ramus	8	3.8—5.5	4.65	.201	12.2	16	4.4—5.6	4.99	.082	6.5
Breadth at M½	18	2.0—2.7	2.24	.044	8.4	25	1.8—2.5	2.16	.043	10.0
Height at M½	16	3.4—5.4	4.46	.128	11.5	24	3.6—5.4	4.33	.115	13.0
P¼ length	6	2.4—2.8	2.58	.060	5.7	7	2.2—2.8	2.66	.081	8.1
M⅓ length	2	2.9—3.0	2.95	.050	2.4	5	2.7—3.2	2.96	.087	6.6
M⅓ post. width	3	1.8—2.0	1.90	.058	5.3	5	2.0—2.3	2.12	.058	6.2
M½ length	5	3.0—3.3	3.18	.058	4.1	8	3.2—3.6	3.48	.049	4.0
M½ post. width	4	2.1—2.4	2.25	.065	5.7	8	2.2—2.4	2.34	.032	3.9
M⅔ length	8	3.0—3.4	3.19	.058	5.2	8	3.0—3.4	3.23	.041	3.6
M⅔ post. width	8	1.9—2.2	2.09	.040	5.4	8	2.0—2.3	2.13	.037	4.9
M¾ length	5	3.2—3.5	3.32	.049	3.3	12	3.2—4.0	3.47	.067	6.7
M¾ post. width	5	0.9—1.4	1.20	.095	17.7	12	1.0—1.4	1.19	.031	9.1
M⅓–¼ length	3	11.9—12.4	12.1	.152	2.2	5	12.4—13.7	12.88	.218	3.8

Of twelve Victoria Cave examples of M^1_1, one showed a short but distinct anterior cingular shelf, six showed a slight depression in the anterior buccal region and in five the anterior wall was continuously smooth. Merrilees (1965) found that one Victorian specimen and two of fifteen from Western Australia showed the anterior-buccal depression on M^1_1. On the basis of one Victorian specimen of *P. gunnii*, Merrilees (1965) believed that a small cingular shelf on M^1_1 might be characteristic of that species, but this is not confirmed by my examination of eleven Tasmanian specimens in the South Australian Museum, in which none has a distinct cingular shelf and only three have an anterior-buccal depression.

P. bougainville was equally abundant in the deposit as *P. gunnii*, but a much higher proportion of *P. bougainville*, the smaller species, was adult (Table 1).

The eastern Australian range of *P. bougainville* at the time of European settlement is poorly known. It occurred on the Liverpool Plains in eastern New South Wales (Ride 1970) and it was apparently abundant near Mildura on the River Murray (Wakefield 1966a). Its remains were found in an owl pellet accumulation of uncertain age in the Grampians, Victoria (Wakefield 1963), but not in other western Victorian cave deposits (Wakefield 1964). In the Fromm's Landing archaeological excavation, it was found from surface level to layers radiocarbon-dated at 2105 ± 85 years BP (Wakefield *in* Mulvaney et al. 1964) but it was not represented in the Mt. Burr archaeological excavation, although *P. gunnii* and *I. obesulus* occurred there (Finlayson 1966 [footnote 1] and personal observations). The Victoria Cave specimens therefore extend the known range of the species in former times into south-eastern South Australia.

In Western Australia, *P. bougainville* survives today only on Bernier and Dorre Islands in Shark Bay (Ride 1970). However, its remains have been found in several caves on the Nullarbor Plain and along the southern half of the west coast of Western Australia (Lundelius 1960, 1963) and in a Pleistocene deposit in Mammoth Cave (Merrilees 1965). It occurred as a modern species in central and western Australia (Ride 1970).

Family **THYLACINIDAE**

Thylacinus cynocephalus (Harris, 1808)

Three isolated teeth are tentatively assigned to this species.

S.A.M. P16120d is a worn canine, probably from a right mandible, with much of the enamel broken away and the root broken. The size (max. antero-posterior length of root 11.8 mm, max. width of root 8.5 mm) is similar to that of modern specimens of *T. cynocephalus* in the South Australian Museum. In the modern specimens the crown is not severely worn, for the upper and lower canines do not meet directly; but the crown of the fossil tooth has either been severely worn, or was broken before death. There is no anterior wear surface such as occurs in many modern specimens of *T. cynocephalus* where I^1_1 meets the lower canine. The fossil tooth is wider relative to its length than are the canines of the dingo (*Canis familiaris* Linnaeus, 1758, var. *dingo* Blumenbach, 1780), its enamel is smooth rather than crenulated as in phocids, and it is more robust than canines of *Sarcophilus harrisii* (Boitard, 1841). I have not examined any *S. laniarus* (Owen, 1838).

S.A.M. P16120h is an incisor, probably a right I^1_1, 3.9 mm wide, 4.3 mm long and with a crown height of 4.6 mm. The root is robust, curved and entered the premaxilla to a depth of 12.9 mm. The occlusal surface is in two planes, the larger surface being the plane of wear against I^1_2, the smaller being the contact surface with the lower canine. The fossil tooth lacks the lateral cuspules found in incisors of *C. f. dingo*, lacks the transverse groove of phocids and is more cuboid than the incisors of *S. harrisii*, where the incisors are crowded and compressed laterally.

A second incisor tooth, S.A.M. P16120j, is probably a right I^1_1. It is 4.3 mm wide, 5.1 mm long and the crown is 3.9 mm high. The root is deep and straight; the tip has been lost. The wear surface is faceted in two planes, the larger being the wear surface against I^1_1, the smaller that against I^1_2. In neither *C. f. dingo* nor phocids are the lower incisors faceted, and in *S. harrisii* the lower incisors are compressed like the uppers.

Additional teeth of *T. cynocephalus* were found associated with remains of a *Protemnodon* (c.f. *P. brehus*) in a rock pile a short distance from the silt deposit. These teeth were almost certainly derived from one individual, and comprise two upper canines, a left mandibular canine, six of the eight upper incisors and all six lower incisors. All are comparable in size to those of modern adult male *T. cynocephalus* in the South Australian Museum but are larger than those of modern adult females.

(*T. cynocephalus* is strongly sexually dimorphic (Ride 1964).)

T. cynocephalus has been extinct on mainland Australia since before European settlement, although it existed then in Tasmania. During the Pleistocene, however, it was widespread on the mainland, as shown by its remains in cave deposits in Victoria, New South Wales, South Australia and south western Australia (Ride 1964).

Family **DASYURIDAE**

Dasyurus maculatus (Kerr, 1792)

The only identified fragment of *D. maculatus* is a broken left maxilla (S.A.M. P16115i) containing the canine alveolus and the six cheek teeth. These do not differ in size or morphology from those of modern specimens. Some tooth dimensions of the fossil are: P^1, length 3.3 mm, width 1.8 mm; P^3, l 4.4 mm, w 2.5 mm; M^1, buccal length 6.1 mm, w 4.3 mm; M^2, bl 6.6 mm, w 5.3 mm; M^3, bl 6.6 mm, w 6.6 mm; M^4, bl 1.6 mm, w 7.2 mm; M^{1-3}, l 19.5 mm.

D. maculatus was not rare in the south-east of South Australia early in this century (Jones 1923, p. 88) but is now extinct in this state (Aitken 1970).

Dasyurus viverrinus (Shaw, 1800)

The skull of *D. viverrinus* can be distinguished from that of the similar-sized *D. geoffroii* Gould, 1841, by the posterior palatal vacuities which are small in *viverrinus* but large in *geoffroii* (Thomas 1888). The posterior palate is not preserved in any Victoria Cave specimen.

The teeth of specimens of the two species in the South Australian Museum, and of Victoria Cave specimens, are similar in size and morphology (Fig. 4), and there is overlap in all linear dimensions of individual teeth and of toothrows. The ratio of the distance from protocone to anterior stylar cusp, to the distance from protocone to posterior stylar cusp, is significantly greater in M^1 and M^3 of *D. geoffroii* than in *D. viverrinus*. (M^1: *D. viverrinus*, ratio = 0.525, *D. geoffroii*, 0.570, $P<.05$ (t test); M^2: *D. viverrinus*, 0.659, *D. geoffroii*, 0.634, not significant; M^3: *D. viverrinus*, 0.664, *D. geoffroii*, 0.733, $P<.05$ (t test)). The ratios in the Victoria Cave specimens are closer to those of *D. viverrinus* (Victoria Cave M^1 ratio, 0.507, M^2, 0.623, M^3, 0.686) and because of this similarity, the Victoria Cave specimens are referred to *D. viverrinus*. Examination of more complete material could possibly alter this decision.

Twenty-one maxillary fragments and 34 mandibular fragments were recovered. Most of the latter lacked teeth and although many isolated teeth were found, none could be fitted to any particular jaw with certainty. Twenty-two of the fragments were from adults, 33 from juveniles. A minimum of seven adults and 12 juveniles are represented. Some dimensions of the teeth are given in Table 6.

TABLE 6

Some dimensions of teeth and alveoli of Dasyurus viverrinus *from Victoria Cave.*

Dimension	n	Range (mm)	Mean	Standard error	Coefficient of Variation
M^1 length	3	5.0—5.7	5.30	.208	6.8
M^2 length	6	5.0—5.5	5.15	.076	3.6
M^3 length	2	5.3—5.4	5.35	.050	1.3
M^4 length	1	1.2	—	—	—
M^{1-3} alveolar length	4	14.5—15.1	14.68	.152	2.1
P^3 alveolar length	4	3.1—4.0	3.4	.196	11.5
M^1 alveolar length	10	3.9—4.9	4.25	.111	8.2
M^2 alveolar length	10	4.2—5.0	4.53	.074	5.2
M^3 alveolar length	14	4.0—5.1	4.44	.071	6.0
M^4 alveolar length	5	4.3—5.3	4.72	.166	7.8
M^{1-4} alveolar length	4	18.0—20.1	19.10	.528	5.5

D. viverrinus is found in many cave deposits in western Victoria (Wakefield 1964) and has been found in the Bat Cave, Naracoorte (Tidemann 1967). The species was formerly common in South Australia (Jones 1923, p. 91) but it is now extinct in this state (Aitken 1970).

Genus ANTECHINUS

Specimens of *Antechinus* were distinguished by the following criteria.

(i) The maxillary molars are more robust, and less compressed antero-posteriorly than in *Sminthopsis*.

(ii) The mandibular fourth premolar is reduced and is always smaller than P_3^3, whereas in *Sminthopsis* and *Antechinomys* P_4^4 is larger than P_3^3.

(iii) Generally the mandible is more robust than in *Sminthopsis* and the masseteric fossa wider. However, some small mandibles of *A. stuartii* are similar in size to those of large *S. murina*.

(iv) The entoconid is always well-developed as it is in *Sminthopsis crassicaudata*. It is much reduced or absent in other species of *Sminthopsis* and in *Antechinomys* (Bensley 1903).

Antechinus flavipes (Waterhouse, 1838)

The mandibular molars of modern specimens of *A. flavipes* in the South Australian Museum are robust, the average width of M_2^2 being 1.34 mm and that of M_3^3, 1.42 mm (Table 7). The length of M_1^1–$_4^4$ is equal to or greater than 7.2 mm and the length of M_1^1–$_3^3$ equal to or greater than 5.5 mm. The premolar teeth are broad and crowded, leaving no spaces between adjacent teeth (Fig. 5).

From Victoria Cave, 10 maxillary and 40 mandibular fragments from a minimum of 23 individuals were indistinguishable in morphology and size from those of the modern specimens of *A. flavipes* (Table 7). All were adults. I have not examined skulls of *Phascogale calura* Gould, 1844 and from published descriptions I cannot exclude the possibility that some of the Victoria Cave mandibles are of that species.

Antechinus flavipes inhabits rainforest, dry sclerophyll forest and woodland, where the animals obtain their insect food from the tree-trunks and large limbs, and from logs. Isolated populations are found in north-eastern Queensland and in south-western Western Australia, while the main population ranges from south-eastern Queensland through eastern New South Wales to Victoria and south-eastern Australia, its distribution being mainly on the inland side of the Great Dividing Range, but extending to the coast at both the northern and south-western extremities (Wakefield & Warneke 1967). Naracoorte is within this range. Remains of *A. flavipes* have been found in the Wombeyan Caves, New South Wales, in a deposit that is probably Upper Pleistocene in age (Ride 1960), but have not been found in Pleistocene (nor Recent) layers of McEachern's Cave, in the extreme south-west of Victoria (Wakefield 1967).

Antechinus stuartii Macleay, 1841

The dentition of *A. stuartii* is identical morphologically with that of *A. flavipes* and, although the former species is on the average much smaller, there is overlap in all dimensions of skull and teeth (Wakefield & Warneke

TABLE 7

Comparisons of some dimensions of teeth and mandibles of Antechinus flavipes *from Victoria Cave with those of a modern sample from southern South Australia and south-western Victoria.*

Dimension	*A. flavipes* from Victoria Cave					Modern *A. flavipes* (n = 18)			
	n	Range (mm)	Mean	Standard error	C.V.	Range (mm)	Mean	Standard error	C.V.
M_2^2–$_3^3$ alveolar length	6	5.9—6.1	5.98	.031	1.3	5.5—6.9	6.12	.087	6.0
M_3^3 width	5	2.1—2.4	2.28	.058	5.7	2.1—2.6	2.36	.030	5.5
Length of ascending ramus	19	4.5—5.9	5.11	.096	8.2	4.5—5.7	5.19	.077	6.3
M_2^2 width	16	1.2—1.4	1.32	.016	5.0	1.2—1.4	1.34	.017	5.2
M_3^3 width	23	1.3—1.5	1.37	.013	4.6	1.3—1.5	1.42	.019	5.5
M_1^1 alveolar length	23	1.5—1.9	1.75	.022	5.9	1.8—2.0	1.88	.015	3.3
M_1^1–$_4^4$ alveolar length	21	7.2—8.1	7.54	.049	3.0	7.2—8.1	7.59	.065	3.7

1967). After measuring modern specimens of both species I have arbitrarily chosen to distinguish as *stuartii* all specimens in which the alveolar length of M^1–^{3} is equal to or less than 5.7 mm and that of M_1–$_4$ is equal to or less than 7.1 mm. In both modern and fossil mandibles the premolars are markedly crowded (Fig. 6), with P_4 often being set obliquely to the line of the jaw.

Six maxillary and 16 mandibular fragments, from a minimum of 11 animals, have been found in Victoria Cave. All but one are adults. They are similar in morphology and size to modern specimens (Table 8).

A. stuartii has not been recorded previously from South Australia, although its present range extends as far west as Portland in Victoria, only 70 km east of the South Australian border (Wakefield & Warneke 1967). Its remains are common in cave deposits in western Victoria where in McEachern's Cave in the extreme south-west, it is found in both Pleistocene (15,200 ± 320 years BP) and Recent layers (Wakefield 1964, 1967).

The present ranges of *A. stuartii* and *A. flavipes* are complementary, the distribution of *stuartii* being coastal to that of *flavipes*, but overlap does occur, e.g. in western Victoria (Wakefield & Warneke 1967).

Antechinus swainsonii (Waterhouse, 1840)

A. swainsonii and *A. minimus* (Geoffroy, 1803) are characterized by their long claws and long snouts. The molar teeth are as long as, or nearly as long as, those of *A. flavipes* (e.g. in 3 specimens of *A. swainsonii* (S.A.M. M2421, M7047 and M7496), M^1–^{3} = 5.5–6.0 mm (mean 5.73), M_1–$_4$ = 7.5–7.8 mm (7.6)], but are much narrower [M^3 = 1.9–2.0 mm (1.97), M_2 = 1.1 mm (in all 3 specimens), M_3 = 1.1–1.2 mm (1.17)]. The premolars too are much narrower than in *A. flavipes* and are not crowded, adjacent teeth often being separated by a space. In addition, the mandibular premolars have long talonids with sharp posterior cuspules, whereas the talonids of *A. flavipes* premolars are short with blunt cuspules. The mandibles of *A. swainsonii* and *A. minimus* are more slender than those of *A. flavipes*, and longer than those of *Sminthopsis* (Fig. 7).

Nine mandibles, from a minimum of five animals, conformed with the *swainsonii-minimus* characteristics, and I have tentatively classified them as *A. swainsonii* because all have a long mandibular symphysis, extending posterior to the front to P_3. The symphysis in *A. minimus* is shorter (Tate 1947). In addition, the greatest breadth of the masseteric fossa in four Victoria Cave specimens ranges from 4.2 to 5.0 mm, whereas in *A. minimus* its greatest breadth does not exceed 4.2 mm (Thomas 1888). In Victoria Cave specimens, the mean width of M_2 is 1.13 mm (3 spec.), mean width M_3 is 1.22 mm (4 spec.) and length M_1–$_4$ ranges from 6.7 to 7.2 mm (mean 7.0) in four specimens.

A. swainsonii has not been recorded alive in South Australia (Aitken 1970), but its remains were found in a late Recent deposit in the Bat Cave, Naracoorte (Tidemann 1967). A single, incomplete, toothless mandible from level 1 of the Fromm's Landing archaeological excavation on the River Murray was assigned

TABLE 8

Comparisons of some dimensions of teeth and mandibles of Antechinus stuartii *from Victoria Cave with those of a modern sample from Bondo, N.S.W.*

Dimension	*A. stuartii* from Victoria Cave					Modern *A. stuartii* (n = 10)			
	n	Range (mm)	Mean	Standard error	C.V.	Range (mm)	Mean	Standard error	C.V.
M^1–^{3} alveolar length	4	5.1—5.7	5.50	.141	5.1	5.3—5.9	5.57	.068	3.9
M^3 width	3	2.0—2.2	2.13	.067	5.4	1.9—2.1	1.96	.022	3.6
Length of ascending ramus	5	4.2—5.4	4.60	.207	10.1	3.9—4.4 n = 7	4.19	.083	5.2
M_2 width	5	1.1—1.3	1.22	.037	6.9	1.1—1.3	1.20	.015	3.9
M_3 width	7	1.2—1.3	1.24	.020	4.3	1.2—1.3	1.27	.015	3.8
M_4 alveolar length	10	1.6—1.8	1.72	.025	4.6	1.5—1.8	1.69	.038	7.1
M_1–$_4$ alveolar length	7	5.8—7.1	6.67	.180	7.2	6.5—7.0	6.85	.052	2.4

to this species (Wakefield *in* Mulvaney et al. 1964). *A. swainsonii* is commonly found in cave deposits in western Victoria (e.g. Wakefield 1964, 1967). On the Australian mainland, *A. minimus* has a limited range around the South Australian-Victorian border near the coast (Wakefield & Warneke 1963).

Genus SMINTHOPSIS

Fragments of *Sminthopsis* were identified by the relatively large P^4 and by the greater antero-posterior compression of the maxillary molars than in *Antechinus*. The mandible is generally more slender than in *Antechinus* and the ascending ramus shorter antero-posteriorly, but there is overlap between *S. murina* and *A. stuartii* in mandible size.

Sminthopsis murina (Waterhouse, 1838)

Mandibles of *S. murina* may be distinguished from those of *S. crassicaudata* (Gould, 1844) by differences in the morphology of the talonids. The entoconids are reduced or absent in *S. murina* but well-developed in *S. crassicaudata* (see Bensley 1903). In the maxillae, interdental fenestrae are smaller and less numerous in *S. murina* than in *S. crassicaudata* (pers. comm. Michael Archer, Western Australian Museum).

In *Antechinomys laniger* (Gould, 1856), which also lacks the entoconid, the postero-external shelf of the lower molars is much broader than in *S. murina*. The dentition of *S. leucopus* is said to be distinguishable from *S. murina* by the presence of spaces between adjacent premolar teeth (Thomas 1888), but this character is variable in the specimens of *S. murina* in the South Australian Museum.

Sixteen maxillary and 57 tooth-bearing mandibular fragments from a minimum of 31 animals were found. Only two were juveniles. A further 61 toothless mandibles, 32 right and 29 left, are probably referable to this species. Some dimensions of the adult specimens and of a modern sample are given in Table 9. The maxillary interdental fenestrae occupied a larger proportion of the interdental space than in many modern specimens and the entoconid was not present in any Victoria Cave mandible. Adjacent premolars, both maxillary and mandibular, usually touched; there was never a conspicuous gap between the premolars (Fig. 8).

In addition to the specimens listed above, one small adult mandible (S.A.M. P16118z) was found that is morphologically identical with *S. murina* but is much smaller, the length of M_1–$_4$ being only 4.8 mm.

S. murina is widespread in South Australia but is nowhere common (Jones 1923, p. 118, Aitken 1970). There is a specimen in the South Australian Museum from Bordertown but Tidemann (1967) did not find this species in a late Recent deposit in the Bat Cave, Naracoorte. The morphologically-similar species, *S. leucopus* (Gray, 1842), is found in Recent, but not Pleistocene layers in McEachern's Cave, extreme south-western Victoria and in other cave deposits in south-western Victoria (Wakefield 1964, 1967).

Sminthopsis crassicaudata (Gould, 1844)

S. crassicaudata was represented by only three mandibles and one maxilla from a minimum of three individuals, all adult. Some dimensions of these are: length of M_1–$_3$, 4.8

TABLE 9

Comparisons of some dimensions of teeth and mandibles of Sminthopsis murina *from Victoria Cave with those of a modern sample from South Australia.*

Dimension	*S. murina* from Victoria Cave				Modern *S. murina* (n = 10)			
	n	Range (mm)	Mean	Standard error	C.V.	Range (mm)	Mean	Standard error	C.V.
M^1–^{3} alveolar length	9	4.6—5.0	4.74	.050	3.2	4.5—5.2	4.76	.062	4.1
M^3 width	9	1.9—2.1	1.98	.022	3.4	1.7—2.0	1.85	.027	4.6
Length of ascending ramus	15	3.5—4.6	4.06	.077	7.3	3.4—4.6	4.05	.137	10.7
M_2 width	17	1.0—1.1	1.05	.012	4.9	0.9—1.1	1.00	.015	4.7
M_3 width	23	1.1—1.2	1.14	.010	4.4	1.0—1.2	1.09	.028	8.0
M_4 alveolar length	30	1.4—1.7	1.48	.014	5.3	1.4—1.8	1.56	.037	7.5
M_1–$_4$ alveolar length	26	5.6—6.3	5.98	.035	3.0	5.5—6.2	5.88	.077	4.2

mm; length of ascending ramus (3 specimens), 3.6–3.9 mm (mean 3.73); M_3 width (3), 1.0 mm; M_4 alveolar length (3), 1.4–1.5 mm (1.43); alveolar length M_1–$_4$ (3), 5.5–5.7 mm (5.67).

This species has a wide range in southern Western Australia, South Australia, Victoria, Western New South Wales and south-western Queensland (Ride 1970), and in the South Australian Museum there are many specimens from the south-east of South Australia. It was found in the Bat Cave deposit, Naracoorte (Tidemann 1967) and in Recent cave deposits in south-western Victoria (Wakefield 1964, 1967).

Discussion

Method of accumulation of the small vertebrate remains.

Analysis of the remains of each species, into adults and juveniles, shows that there is considerable variation between species in the proportion of adults. The larger species, *Bettongia penicillata* and *Potorous apicalis*, are represented almost entirely by juveniles (Smith 1971), as is the large bandicoot, *Perameles gunnii*. Adults and juveniles of smaller species, such as *Isoodon obesulus* and *Potorous platyops*, were found in about equal numbers, while the small dasyurids (*Antechinus* and *Sminthopsis*) and the petaurids and burramyids were nearly all adults. Slower eruption of the teeth in the larger species may account for some of this variation, but it does not account for the wide variations seen between two species of the one genus. For example, within *Perameles* no more than one quarter of the larger *P. gunnii* were adults, but more than half of the smaller *P. bougainville* were adults.

The biased age structure suggests that the cave did not act as a simple pitfall trap, but that the bones were brought in by predators able to capture animals as large as an adult *P. bougainville* or *Potorous platyops*, or a juvenile *P. gunnii* or bettong. Mammal predators that inhabit dens usually die within them occasionally. *Thylacinus cynocephalus* was able to take larger prey (Ride 1970) and so the predators could have been dasyurids, *Dasyurus maculatus* or *D. viverrinus*, or owls. The very low incidence of *D. maculatus* suggests that this species was not the predator. *D. viverrinus* is better represented but the high proportion of juveniles indicates that it was a prey species rather than a predator. The small mammals therefore probably accumulated from owl pellets. The method of accumulation of the large herbivores in the deposit is not yet known.

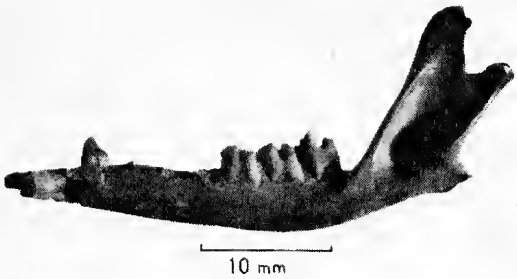
Climatic interpretations

Modern populations of the scansorial species *Antechinus flavipes* and *A. stuartii* are sympatric in areas of dry sclerophyll forest such as at Glenlofty, western Victoria, where stringybark (*Eucalyptus macrorrhyncha*) and box (*E. melliodora* and *E. goniocalyx*) are associated with a sparse ground cover of sawsedge (*Gahnia radula*) and tussock grass (*Poa*) (Wakefield & Warneke 1967). Populations of the ground-dwelling *A. swainsonii* are densest in wet sclerophyll forest, but they also occur in other habitats such as open woodland and stunted coastal eucalypt scrub with tussock grass (Wakefield & Warneke 1963).

Modern *Sminthopsis murina* and *S. crassicaudata* inhabit both wet and arid areas and little is known of their habitat requirements. *Perameles bougainville* was similarly wide ranging at the beginning of European exploration, and its habitat requirements are also unknown.

P. gunnii and *I. obesulus* occur sympatrically in Tasmania. Both species require scrub for nesting and the food of both consists mainly of earthworms and insect larvae. However, *Isoodon* remains within the scrub to feed, whereas *Perameles* forages far out into open areas (Heinsohn 1966). If the Pleistocene *Perameles* and *Isoodon* had similar ecological requirements to their modern descendants, one might infer that the apparent scarcity of *Isoodon* indicated that the vegetation of the area was an open woodland, with little dense scrub. On the other hand, the greater abun-

Fig. 1. Left mandible of *Isoodon obesulus* (S.A.M. P16112x) from Victoria Cave.
Fig. 2. Right mandible of *Perameles gunnii* (S.A.M. P16104v) from Victoria Cave.
Fig. 3. Left mandible of *Perameles bougainville* (S.A.M. P16103f) from Victoria Cave.
Fig. 4. Left maxilla of *Dasyurus viverrinus* (S.A.M. P16115a) from Victoria Cave, occlusal view of M^1 to M^4.
Fig. 5. Right mandible of *Antechinus flavipes* (S.A.M. P16001j) from Victoria Cave.
Fig. 6. Right mandible of *Antechinus stuartii* (S.A.M. P16119i) from Victoria Cave.
Fig. 7. Right mandible of *Antechinus swainsonii* (S.A.M. P16009a) from Victoria Cave.
Fig. 8. Right mandible of *Sminthopsis murina* (S.A.M. P16021a) from Victoria Cave.



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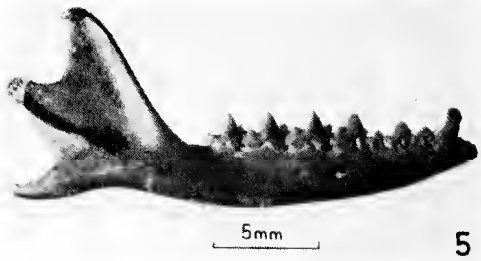

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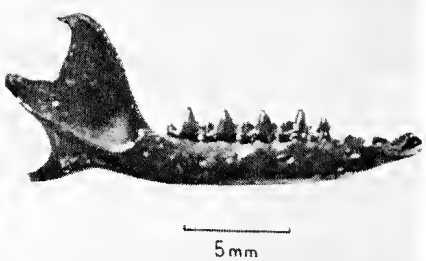

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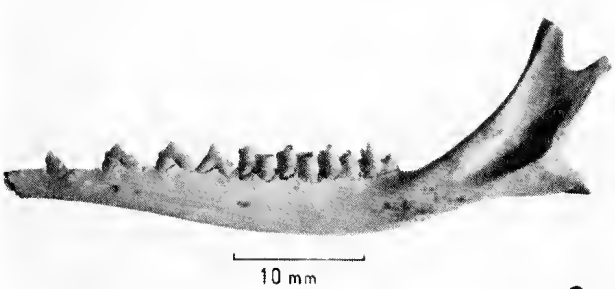

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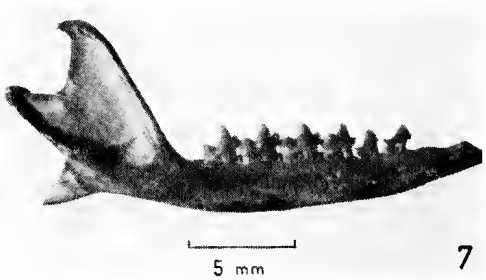

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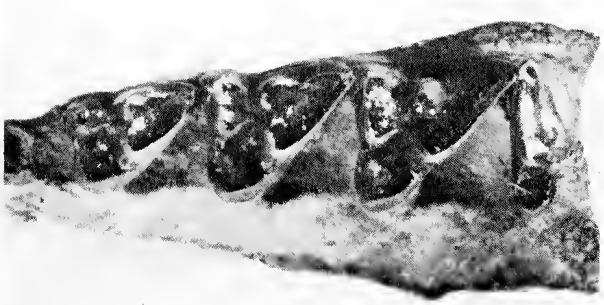

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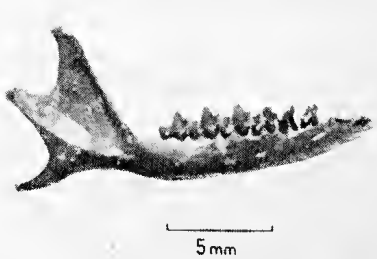

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dance of *Perameles* might be an artefact of selective predation, for animals foraging in scrub would be less susceptible to owl attack than animals foraging in the open. However in the Mammoth Cave deposit, *P. bougainville* is about twice as abundant as *I. obesulus*. This is believed to be a true reflection of a larger population of *Perameles* in the Pleistocene, for the deposit does not seem to have originated from owl pellets, but appears to have been a talus deposit, accumulating as animals fell through holes in the roof (Merrilees 1965).

The combined evidence of the represented species of potoroines, petaurids and burramyids (Smith 1971) and of the peramelids and dasyurids indicates that at the time of accumulation of the deposit Victoria Cave was surrounded by dry sclerophyll forest.

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